

Temporal Patterns of Nudibranch Mollusk Activity on a Subtidal Hawaiian Reef

by

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Abstract. Differences in abundance and diversity of nudibranchs based on day and night sampling on the same shallow subtidal Hawaiian reef are documented. Species active during the day tend to be brightly colored and contrast with their surroundings, while those active at night are more likely to possess cryptic coloration. Abundance is greater during day sampling, but diversity is substantially greater at night.

INTRODUCTION

Nudibranchs are soft-bodied animals capable of secreting themselves in holes and cracks so effectively that they are often overlooked by even the most careful observer. Frequently, one or more nudibranchs completely invisible during a thorough external examination of a rock will suddenly appear after that rock is placed into an aquarium. This characteristic of nudibranchs could conceivably affect the results of nudibranch population studies such as that of NYBAKKEN (1978), who calculated diversity based upon numbers found by visual examination of rocks. If one or more species that typically hide in small cracks and holes experienced population fluctuations, it could have affected Nybakken's conclusions. Nybakken was aware of this possibility; he pointed out the difficulty of sampling some of the smaller, more cryptic species. Similarly, POTTS (1970) admitted that estimates of abundance during his study were low due to inaccessibility of some rock crevices.

The study arose from the observation that nudibranch species never or rarely observed during the day could be found easily at night. According to HARRIS (1973), "... in Hawaii . . . a number of species . . . are photonegative and nocturnal, but many more are active during the day." However, observations made during day and night scuba dives on a shallow subtidal reef off the island of Oahu, Hawaii, suggested that more species could be found at night than are typically found during the day. This study was undertaken to: (1) verify the observation that the sampled nudibranch assemblage differs depending on the time of day that sampling takes place, and (2) try to determine whether nocturnal nudibranch sampling would be a way to obtain a more accurate estimate of nudibranch populations.

METHODS

The location and characteristics of the sampling site are described in JOHNSON (1983). Briefly, the study reef is at Makua (21°32'50"N, 158°13'32"W) on the western shore of Oahu, Hawaii. The reef is on the southern face of a basaltic peninsula extending outward from shore. The site consists of a subtidal vertical cliff, 200 to 300 m in length and varying in depth from 2 to 6 m. The cliff forms a nearly complete circle, offering a gradient of exposure to wave action. The cliff face is pocketed with innumerable holes, caves, and ledges, most of which are thickly encrusted with sponges and other sessile organisms.

Preliminary sampling to determine major differences was done by timed swims along the study cliff, carefully examining the path for nudibranchs. A total of 52 h of timed-swim counting was done during the day and 34 h at night.

For a more direct comparison, 12 permanent and 25 randomly chosen m² quadrats were sampled. All quadrats were carefully and thoroughly searched for nudibranchs on each of six different sampling expeditions. The same 12 permanent quadrats were sampled on each expedition to the study site; these 12 quadrats were selected to be approximately equidistant around the study reef and were all ledges or small caves with high cover of sponges and other encrusting organisms (the most likely areas to find nudibranchs in Hawaii; see BERTSCH & JOHNSON, 1982). The 25 random quadrats were chosen anew on each of the six expeditions (see JOHNSON, 1983, for a description of how the quadrats were selected). For each expedition, the same permanent and random quadrats were sampled once during the day and again that night.

Within each quadrat, the number of nudibranchs of each species was noted, as well as the substrate beneath each individual and whether or not the nudibranch was feeding. Also, each species observed was judged to be cryptic or

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flamboyant based on how easy it was to see in its typical surroundings.

Note that this difference between cryptic and flamboyant is highly subjective and depends upon a number of factors. First, it assumes that observations are made during the day; in the dark, all species are cryptic. Second, substrate is important. A nudibranch highly cryptic on one substrate may be flamboyant on another. Third, depth may also be a factor. As colors fade with increasing depth, what is a flamboyant color pattern in shallow water may become a camouflaged pattern on the same substrate in deeper water. The decisions on cryptic or flamboyant in this paper are based solely upon how the nudibranch appeared in its usual habitat in the Makua site, which is shallow enough for all or most colors to be visible during the day.

Shannon-Wiener diversity indices (H) were calculated for both day and night samples using the formula:

$$H = - \sum_{i=1}^s p_i (\ln p_i)$$

where p_i is the proportion of the i th species and s is the number of species. Equitability (J), the "evenness" of the abundances of the various species, is defined as:

$$J = H / (\ln s)$$

T -tests were performed to determine whether the mean diversity differed between the day and night samples.

RESULTS

In 52 h of timed swims along the study reef during the day, 3081 nudibranchs representing 25 species were observed, yielding an average of 59.3 nudibranch individuals per search hour. In 34 h at night, 1898 nudibranchs spread over 44 species were observed, for an average of 55.8 per hour.

Table 1 shows the breakdown of species and abundances for all 222 quadrats sampled both day and night. In the day quadrats, 465 individuals of 17 species were counted; at night, the count totalled 407 individuals of 26 species. In the column labeled "Visibility," "flamboyant" indicates that the nudibranchs were easy to see in typical surroundings; "cryptic" means that they were difficult to see or hard to recognize as nudibranchs (even using a flashlight at night).

Table 2 summarizes the numbers of the five most common species found during the day and night quadrat sampling. Only two species are present on both lists. The other three species on each list show considerable disparity in abundances between day and night.

Shannon-Wiener indices and equitability statistics calculated for the day and night quadrat samples are compared in Table 3 for each of the six sampling expeditions. A t -test comparing mean diversity between day and night shows differences to be significant ($t = 6.1429 > 3.169 = t_{10,0.005}$). Mean equitability between day and night also differs significantly ($t = 4.3416 > 3.169 = t_{10,0.005}$).

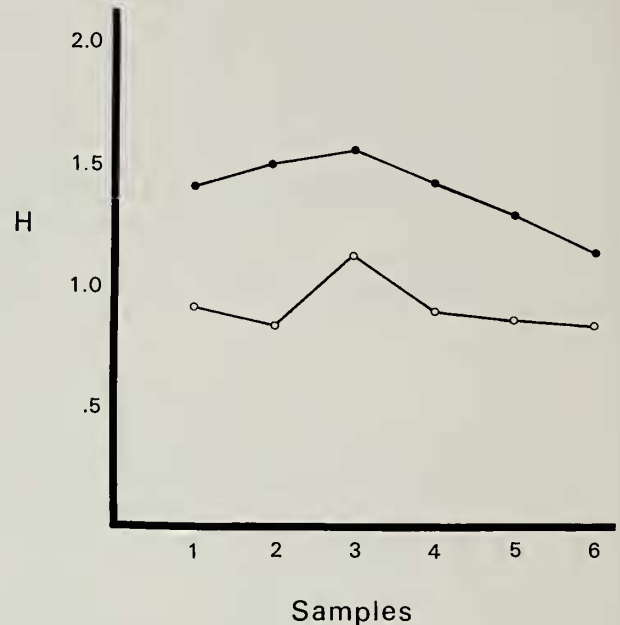


Figure 1

Diversity (H) of day (open circles) and night (closed circles) samples over the study period.

A merged count of nudibranchs was made using the larger of the day or night numbers counted for each species observed in the quadrats on a particular sampling expedition (e.g., if 15 specimens of a species were counted during the day and 10 at night, the day figure was used; if more were found at night than during the day, the night figure was used). Shannon-Wiener and equitability statistics were also calculated for these merged samples (Table 3). Calculated diversity is greater for the merged samples than for either the night or day samples alone.

DISCUSSION

Abundances

Both timed-swim and quadrat counts reveal large differences in the species observed and their relative abundances. Although more species are observed at night, the overall number of nudibranchs counted is greater during the day. This is due primarily to the reduced numbers of the two most abundant species at night.

Glossodoris rufomarginata (Bergh, 1890) (= *Chromolaichma youngbleuthi* (Kay & Young, 1969) in JOHNSON, 1983), although by far the most abundant nudibranch at all times, is less frequently observed in the same quadrats at night than during the day. The animals' behavior explains this difference. During the day, specimens of this small (2–30 mm), brown-speckled nudibranch are nearly always observed preying upon a massive, dark gray to black sponge that lives in ledges along the cliff face (JOHNSON, 1983); 82.6% of the individuals observed during the day were on

Table 1
Nudibranchs observed in 222 1-m² quadrats along the Makua reef.

Species	Day		Night		Visibility
	Total no.	% of total	Total no.	% of total	
<i>Glossodoris rufomarginata</i> (Bergh, 1890)	334	71.83	264	64.86	flamboyant
<i>Hypselodoris</i> sp. 1 ^a	82	17.63	10	2.46	flamboyant
<i>Aldisa pikokai</i> Bertsch & Johnson, 1982	0	0.00	34	8.35	cryptic
<i>Halgerda terramtuensis</i> Bertsch & Johnson, 1982	6	1.29	13	3.19	cryptic ^b
<i>Sclerodoris paliensis</i> Bertsch & Johnson, 1982	0	0.00	17	4.18	cryptic
<i>Chromodoris</i> sp. 1	0	0.00	13	3.19	cryptic
<i>Chromodoris</i> sp. 2 ^c	4	0.86	7	1.72	flamboyant
<i>Chromodoris vibrata</i> (Pease, 1860)	7	1.51	3	0.74	flamboyant
<i>Phidiana indica</i> (Bergh, 1896)	4	0.86	5	1.23	flamboyant
<i>Hypselodoris</i> sp. 2 ^d	8	1.72	0	0.00	flamboyant
<i>Hexabranhus sanguineus</i> (Rüppell & Leuckart, 1828)	1	0.22	7	1.72	flamboyant
<i>Hypselodoris</i> sp. 3	5	1.07	2	0.49	flamboyant
<i>Chromodoris albopustulosa</i> (Pease, 1860)	3	0.65	3	0.74	flamboyant
<i>Phyllidia varicosa</i> Lamarck, 1801	2	0.43	4	0.98	flamboyant
<i>Phestilla melanobrachia</i> Bergh, 1874	2	0.43	4	0.98	cryptic
<i>Chromodoris</i> sp. 3 ^e	1	0.22	3	0.74	flamboyant
<i>Chromodoris albopunctata</i> (Garrett, 1879)	1	0.22	2	0.49	flamboyant
<i>Jorunna alisonae</i> Marcus, 1976	0	0.00	3	0.74	cryptic
<i>Plocamopherus</i> sp. ^f	0	0.00	3	0.74	cryptic
<i>Pteraeolidia ianthina</i> (Angas, 1864)	2	0.43	1	0.25	flamboyant
<i>Chromodoris</i> sp. 4	2	0.43	0	0.00	flamboyant
<i>Phyllidia pustulosa</i> Cuvier, 1804	1	0.22	1	0.25	flamboyant
<i>Dendrodoris</i> sp. aff. <i>rubra</i> (Collingwood, 1881)	0	0.00	2	0.25	flamboyant
<i>Okenia</i> sp.	0	0.00	2	0.49	cryptic
<i>Chromodoris aspersa</i> (Gould, 1852)	0	0.00	1	0.25	flamboyant
<i>Sclerodoris</i> sp. ^g	0	0.00	1	0.25	cryptic
<i>Phyllidia</i> sp. 2 ^h	0	0.00	1	0.25	flamboyant
<i>Bornella</i> sp.	0	0.00	1	0.25	cryptic

^a "Locust" in BERTSCH & JOHNSON, 1981 (B & J).

^b Could be considered cryptic or flamboyant.

^c *Chromodoris albonotata* in B & J.

^d *Hypselodoris lineata* in B & J.

^e "Snowflake" in B & J.

^f *Plocamopherus tilesii* in B & J.

^g *Halgerda rubra* in KAY & YOUNG, 1969.

^h "Blue-black *Phyllidia*" in B & J.

the rather smooth-surfaced sponge, against which they were conspicuous. At night, individuals of this species had a tendency to move off the sponge. Only 43.2% of the *G. rufomarginata* observed at night were on the prey sponge; the rest were usually on the hard, irregularly shaped reef surfaces near the sponge colonies. (Percentages on prey sponges were obtained from the quadrat data only.) *Glossodoris rufomarginata* individuals observed at night were generally contracted and quiescent, rarely crawling, and never actively feeding. These observations suggest that *G. rufomarginata* is a day-active species. The numbers observed at night, however, indicate that individuals of this species do not effectively hide when they are not active.

The second most abundant species, *Hypselodoris* sp. 1 (=chromodorid 1 in JOHNSON, 1983), is also active during the day. Contrasting with *Glossodoris rufomarginata*, however, *Hypselodoris* sp. 1 hides very well at night.

During the day, *Hypselodoris* sp. 1, a small (2–15 mm) nudibranch, is commonly observed actively crawling or feeding, often in aggregations, on a bright yellow sponge. Occasionally, aggregations of 30 or more individuals totally devour a colony of the sponge down to the calcareous or basaltic substrate (JOHNSON, 1983). This process of decimating an entire sponge colony often takes weeks; yet night observations of a colony being preyed upon always reveal no nudibranchs. To determine where the nudibranchs go after dark, one aggregation of 34 individuals on a sponge colony was watched from late afternoon into early evening. About 1½ h before sunset, as the light level on the reef was diminishing, one individual of *Hypselodoris* sp. 1 crawled about 10 cm from the chunk of sponge it had been eating and disappeared into a small crack in the reef. (This crack was located in a bare patch of reef that previously had been covered by the yellow prey sponge,

Table 2

Comparison of the five most abundant diurnal and nocturnal nudibranchs in the 222 1-m² quadrats.

Day		Night	
Species	No.	Species	No.
<i>Glossodoris rufomarginata</i>	334	<i>Glossodoris rufomarginata</i>	264
<i>Hypselodoris</i> sp. 1	82	<i>Aldisa pikokai</i>	34
<i>Hypselodoris</i> sp. 2	8	<i>Sclerodoris paliensis</i>	17
<i>Chromodoris vibrata</i>	7	<i>Chromodoris</i> sp. 1	13
<i>Halgerda terramtuensis</i>	6	<i>Halgerda terramtuensis</i>	13

but which had been grazed clean.) Others followed along the same track at irregular intervals, possibly following a mucous trail. By sunset, the few nudibranchs not already in the crack were actively moving. By dark, not a single specimen was visible. All had vanished into the same crack in the reef. When the sponge colony was next examined, at approximately 11 A.M. the next morning, 32 *Hypselodoris* sp. 1 individuals could be counted on and in the sponge.

The behavior of moving away from the prey sponge and into a hole in the reef was later observed during several other dusk observations.

Only 10 individuals of *Hypselodoris* sp. 1 were observed in the quadrats at night as opposed to 82 during the day. Of the 10 observed at night, nine were packed together in a small hole in the reef next to a sponge colony that earlier that day was observed being preyed upon by 29 specimens of *Hypselodoris* sp. 1.

Species active exclusively at night include *Chromodoris* sp. 1, *Aldisa pikokai* Bertsch & Johnson, 1982, and *Sclerodoris paliensis* Bertsch & Johnson, 1982. No individuals of these species were observed during day sampling; yet, these three were among the most frequently observed species at night.

Predation and Warning Coloration

Why is there such a disjunct pattern of day and night activity among nudibranchs on this reef? Two possible answers are ease of feeding and predator avoidance. The former can probably be discounted. Of the 28 species in Table 1, 23 are sponge predators, two eat hydroids, one preys upon hard corals in the genus *Tubastraea*, and at least one eats bryozoans (feeding data from KAY & YOUNG, 1969; BLOOM, 1976; BERTSCH & JOHNSON, 1981; JOHNSON, 1983; and personal observations). All these prey items are sessile and attached to the substrate; they should be no easier to "catch" during the day or night. It is possible that each nudibranch species is most active when its prey's defenses are at a minimum (e.g., if production of sponge toxins varies between day and night). This possibility was not tested but does not seem likely.

The question of predator avoidance is more difficult to assess. Nudibranchs may avoid predation by being dis-

tasteful or poisonous, or by being hard to find. The nudibranchs in the Makua study site range into both extremes of visibility; there are brilliantly colored species that contrast sharply with their surroundings, and there are extremely cryptic species that are very difficult to see.

The presence of brilliantly colored species raises the possibility of warning coloration. Warning coloration has been suggested many times to explain nudibranch coloration (e.g., GARSTANG, 1890). However, as THOMPSON (1960) correctly pointed out, it is dangerous to assume that warning coloration exists without being able to show that potential predators hunting by vision avoid the color pattern in question, and that the prey has some characteristic making them unpalatable. In THOMPSON's (1960) laboratory experiments, certain fish species refused all healthy individuals of cryptic and non-cryptic opisthobranchs, but readily accepted damaged specimens, suggesting that coloration is not important in deterring predators.

Laboratory experiments, however, cannot show that fish or other predators never eat opisthobranchs in nature, and natural observations are difficult to make. Except in certain cases (such as an animal grazing upon a sessile organism), acts of predation in the marine environment are rarely observed; the amount of time a predator spends actually consuming a prey is small compared to the total time hunting or doing other things. An act of predation upon a nudibranch, if it occurs, is likely to be of very short duration and to leave no tell-tale evidence (e.g., the empty or crushed shell of a prosobranch gastropod). It may take many hours of observation to encounter predation upon a nudibranch even once, especially if the potentially cryptic coloration or toxic defenses are effective.

Despite the difficulty of observing natural predation, I have witnessed what appeared to be predation upon nudibranchs in the Makua site twice, both at night. In one case, a spiny lobster, *Panulirus marginatus* (Quoy & Gaimard, 1825), attacked and consumed an apparently healthy *Hexabranchnus sanguineus* (Rüppell & Leuckart, 1828). In the other, a portunid crab, *Charybdis orientalis* Dana, 1852, was observed eating a *Dendrodoris elongata* Baba, 1936. In the latter example, the attack of the predator was not observed; only the fact that the crab was eating the nudibranch. The nudibranch could have been dead, dying, or damaged before the crab began to eat it. (*Dendrodoris*

Table 3

Comparison of the Shannon-Wiener Index (H) and Equitability (J) between day, night, and "merged" quadrat samples.

Sample	Day		Night		Merged	
	H	J	H	J	H	J
1	0.9169	0.4712	1.4001	0.5459	1.5532	0.5602
2	0.8465	0.4350	1.5171	0.5749	1.6332	0.5891
3	1.1491	0.4990	1.5597	0.6504	1.6878	0.6233
4	0.9004	0.4330	1.4293	0.5752	1.5574	0.5751
5	0.8668	0.3945	1.2970	0.5220	1.5294	0.5516
6	0.8325	0.4646	1.1557	0.5019	1.3895	0.5265

elongata is a nocturnal species observed several times on the timed swims, but was never present in any of the sampled quadrats.)

There is evidence that visual predators attack healthy nudibranchs in other areas. In Micronesia (Enewetak Atoll, Marshall Islands), labrids of the genus *Thalassoma* approached to within 25 cm of my face mask to decimate a group of the cryptic *Phestilla lugubris* (Bergh, 1890) on the underside of an overturned rock. Similarly, TODD (1981) reported labrids voraciously feeding upon small nudibranchs and sacoglossans on the exposed undersurfaces of rocks.

These observations suggest that predation can and does occur on nudibranchs in nature; only the extent is unknown. Given that some predation occurs, the present study provides circumstantial evidence that warning coloration does play a part. If it is assumed that diurnal species are those more than twice as likely to be found during the day and nocturnal species more than twice as likely to be found at night, Table 1 indicates that colorful species such as chromodorids and phyllidiids tend to be diurnal, while cryptic species are more likely to be nocturnal.

Several species require further comment. Although *Glossodoris rufomarginata* is not twice as likely to be found during the day than at night, it was already shown to be day active. Extensive observations of all the different species of *Phyllidia* and many species in the family Chromodorididae indicate that these species may be found with equal ease either day or night. Finally, *Halgerda terramtuensis* may be either cryptic or flamboyant on typical substrates. Against yellow sponge or multicolored sponge backgrounds, *H. terramtuensis* is cryptic; on hard reef coated with purplish encrusting algae, it contrasts sharply and is easy to see.

Some species are known to possess anti-predator defenses. Secretions from *Phyllidia varicosa* Lamarck, 1801, are known to kill other animals (JOHANNES, 1963), and the toxic compounds found in *P. varicosa* occur in other species of *Phyllidia* as well (G. Schulte, personal communication). *Dendrodoris tuberculosa* (Quoy & Gaimard, 1832), a species found in the day timed swims but not in the quadrats, produces secretions irritating to human eyes (BERTSCH & JOHNSON, 1981). *Pteraeolidia ianthina* (An-

gas, 1864) feeds upon hydroids and stores rather potent nematocysts in their ceratal tips (BERTSCH & JOHNSON, 1981). Chromodorids in general are characterized by large glands along the mantle margin (EDMUNDS, 1981; RUDMAN, 1984) which may be defensive in nature.

Observations in other areas indicate that predators avoid certain nudibranchs. At Magic Island, Oahu, Hawaii, many individuals of the flamboyantly colored *Risbecia imperialis* (Pease, 1860) (= *Chromodoris godeffroyana* (Bergh, 1879)) in JOHNSON & BERTSCH, 1979, and BERTSCH & JOHNSON, 1981) possess healed wounds that appear to be bite marks (personal observation). If these highly conspicuous, always exposed nudibranchs were palatable, it is likely that fewer would be bitten only once and left to heal. At Enewetak, the same individuals of *Thalassoma* that readily preyed upon *Phestilla lugubris* (described above) ignored a brightly colored *Chromodoris fidelis* (Kelaart, 1858) under the same rock.

Many nudibranchs are known to contain organic compounds that may be toxic to predators (e.g., SCHULTE *et al.*, 1980; SCHULTE & SCHEUER, 1982; FAULKNER & GHISELIN, 1983; OKUDA & SCHEUER, 1985). Examining the literature on chemical studies suggests that most experiments have been performed on those that fall into the flamboyant category rather than on those that are more cryptic.

While most chromodorids are less common (or at least, not significantly more common) at night than during the day, one undescribed chromodorid species encountered in this study, *Chromodoris* sp. 1, is strictly nocturnal. This nocturnal species possesses uncharacteristically (for a chromodorid) dull coloration, with translucent grayish spots on a white background and a faint yellow tinge to the margin. From a distance, the nudibranch resembles one of the reef's common sponges, which is oval and white with faint spots.

Some of the other abundant nocturnal species are extremely cryptic, even when illuminated with a bright light. *Aldisa pikokai* and *Sclerodoris paliensis*, while bright red and yellow respectively, strongly resemble clumps of sponge and are difficult to recognize as nudibranchs (see color photographs of *Aldisa* sp. and *Sclerodoris* sp. in BERTSCH & JOHNSON, 1981:44-45). At least to humans, these and

several other nocturnal species are extremely cryptic. If a species must hide from view (either by cryptic coloration, nocturnal habits, or both), it seems reasonable that it might not possess chemical defenses.

The next logical step would be to try to locate predators that would eat these nocturnal species and also to examine more of the cryptic species for unusual organic compounds that affect potential predators. Additionally, these organic compounds must be shown to protect the nudibranchs from predation; as SCHULTE & SCHEUER (1982) point out, it has not been demonstrated in most cases that organic compounds found in nudibranchs do in fact repel predators.

A lack of chemical defenses in the cryptic or nocturnal species contrasting with the presence of such defenses in brightly colored diurnal species would add more evidence both for the existence of warning coloration in nudibranchs and for predator avoidance as a major reason for the difference between day and night activity.

Diversity

NYBAKKEN (1978) reviewed some of the controversy regarding which diversity index is preferable. He chose the Brillouin index because of his not completely random sampling data, and because he was interested only in local diversity in a particular area and its variation. He also computed the Shannon-Wiener index for comparison and found that the two indices, at least for his data, were closely correlated. In the present study, the Shannon-Wiener index was used for ease of calculation with the rather large numbers involved. Whether or not the index gives a "true" estimate of diversity, it is certainly adequate for comparing the relative diversity of day and night samples.

Because of the larger numbers, it is tempting to use the data from the timed swims for the diversity calculations. However, the differences in total search times between night and day, and the biases inherent in a haphazard searching technique, make these data unacceptable for such statistical analyses. Using the haphazard sampling technique represented by the timed swims, one is far more likely to miss a 4-mm long, white *Okenia* sp. than a 200-mm, bright red *Hexabranhus sanguineus*. Careful searching of limited quadrats yields a far more realistic estimate of nudibranch proportions.

The greater diversity and equitability observed on the Makua reef at night substantiates the observation that there is a significant amount of nocturnal activity in addition to what is observed during the day. This points out clearly that, at least for this reef, daytime sampling is insufficient for determining the numbers and proportions of the different nudibranch species present. Because of day-active species that hide at night (such as *Hypselodoris* sp. 1), nocturnal sampling is also inadequate. A more realistic estimate of abundances might be obtained by sampling both day and night, and using the larger of the two counts obtained for each species (e.g., the column labeled "Merged" in Table 3).

It might be argued that combining the different samples to produce the merged statistics is invalid. However, because of the differences in activity, it could equally be argued that the day or night counts alone produce diversity values that are at best unacceptable and at worst meaningless. While not an exact representation of the true diversity, the merged value is based on a better minimum abundance of each species present and should therefore be a closer estimate of the actual diversity.

Comparison of the results of this study with similar observations from other areas is useful. Personal observations at Enewetak, Marshall Islands, west central Pacific, suggest that the day vs. night difference in activity is not nearly as pronounced as on the Makua reef. Nearly all species of nudibranchs at Enewetak tend to hide during the day, perhaps owing to the effects of higher levels of solar radiation on prey sponges (see JOKIEL, 1980, and the discussion of the "inside-out phenomenon" in BERTSCH & JOHNSON, 1982). Examination of temporal differences in activity by different species might be most interesting in a place such as southern California, where numerous subtidal nudibranch species and their prey are found completely exposed in the daytime.

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